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# Seasonal shoot and needle growth of loblolly pine responds to thinning, fertilization, and crown position

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**Abstract**

The impacts of thinning, fertilization and crown position on seasonal growth of current-year shoots and foliage were studied in a 13-year-old loblolly pine (*Pinus taeda* L.) plantation in the sixth post-treatment year (1994). Length of new flushes, and their needle length, leaf area, and oven-dry weight were measured in the upper and lower crown from March through November. Total shoot length was the cumulative length of all flushes on a given shoot and total leaf area per shoot was the sum of leaf areas of the flushes.

By the end of June, first-flush foliage reached 70% of the November needle length (14.3 cm) and 65% of the final leaf area (15.0 $cm^2$). Cumulative shoot length of first- and second-flush shoots achieved 95% of the annual length (30.3 cm), whereas total leaf area per shoot was 55% of the final value (75.3 $dm^2$). Fertilization consistently stimulated fascicle needle length, dry weight, and leaf area in the upper crown. Mean leaf area of upper-crown shoots was increased by 64% six years after fertilization. A significant thinning effect was found to decrease mean leaf area per shoot in the crown. For most of the growing season, the thinned-fertilized trees produced substantially more leaf area per shoot throughout the crown than the thinned-nonfertilized trees. These thinned-fertilized trees also had greater needle length and dry weight, longer first flush shoots, and more leaf area per flush than trees in the thinned-nonfertilized plots. Needle length and leaf area of first flush shoots between April and July were linearly related to previous-month canopy air temperature ($T_a$). Total shoot length strongly depended on vertical light gradient (PPFD) within the canopy, whereas shoot leaf area was a function of both PPFD and $T_a$. Thus, trees produced larger and heavier fascicles, more and longer flush shoots, and more leaf area per shoot in the upper crown than the lower crown. We conclude that thinning, fertilization, and crown position regulate annual leaf area production of current-year shoots largely by affecting the expansion of first flush shoots and their foliage during the first half of the growing season. © 1999 Elsevier Science B.V. All rights reserved.

*Keywords:* First flush shoots; Shoot expansion; Fascicle needle size; Leaf area; Treatment effect; *Pinus taeda* L.

## 1. Introduction

The photosynthetic surface area of a tree depends on quantity and spatial distribution of foliage in the crown (Russell et al., 1989). Shoot structure and

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needle morphology are closely correlated with tree growth and stand productivity by their effects on the efficiency of light interception within the canopy (Leverenz and Hinckley, 1990; Jordan and Smith, 1993; Niinemets and Kull, 1995; Sprugel et al., 1996; Stenberg, 1996). Recent studies also indicate that silvicultural practices such as thinning and fertilizing may increase foliage production, crown development, tree size, and root growth in many conifers (Brix, 1981, 1982; Binkley and Reid, 1984; Shelburne et al., 1993; Teskey et al., 1994; Dougherty et al., 1995; Sheriff, 1996; Sword et al., 1996). Vose (1988) found that leaf area of loblolly pine at the tree and stand level was dramatically increased after fertilization. Stemwood volume was increased with increasing leaf area index (LAI), and variation in stand LAI was associated with stand density and nitrogen availability (Vose and Allen, 1988). Thinning, on the other hand, increases live crown diameter (Ginn et al., 1991; Peterson et al., 1997), and leaf biomass (Gillespie et al., 1994). Thinning and fertilization combinations also increase branch foliage biomass, but they do not necessarily change the vertical distribution of foliage in the crown (Gillespie et al., 1994). Needle photosynthesis and stomatal conductance of loblolly pine foliage in the lower crown respond positively to reduced stand density (Nowak et al., 1990; Ginn et al., 1991; Gravatt et al., 1997; Peterson et al., 1997; Tang et al., 1998). In addition, fertilizer applications may have variable effects on needle physiology (Murthy et al., 1996, 1997; Zhang et al., 1997; Tang et al., 1998).

Little is known about seasonal responses of coniferous needle production and shoot growth to thinning and fertilization. Studies with older trees are needed to understand how silvicultural treatments control seasonal crown development, shoot phenology, and foliage morphology of pine trees. This information will be valuable for the scaling of physiological responses from needle to shoot, branch, and crown levels in relation to cultural treatments (Gravatt et al., 1997). Field data may also help provide better models for the changing climate conditions (Sword et al., 1998). The objectives of this portion of our study were to: (1) examine the effects of thinning, fertilization, and crown level on current-year shoot and needle expansion, and leaf area growth in a 13-year-old loblolly pine plantation six years after treatment; and (2) determine relationships between early-season fascicle and shoot growth and the branch micro-environment within the treatment plots. We hypothesize that foliage and shoot morphology and leaf area production in a pine stand respond to thinning, fertilization, and crown position.

## 2. Materials and methods

### 2.1. Site description and silvicultural treatments

The study site is a 0.93 ha area located in the Palustris Experimental Forest of Rapides Parish, Louisiana, USA (31°11′ N, 92°41′ W). The soil at the site is a well drained Beauregard silt loam with a gentle slope. In May 1981, the plantation was established (1.8×1.8 m) with 14-week-old containerized half-sib loblolly pine seedlings. At the end of 1987, survival was 97% and tree size was uniform across the plantation (Haywood, 1994).

Twelve plots were established in the spring of 1988. Each plot was 23.8×23.8 m (0.06 ha) and consisted of 13 rows of 13 trees. Thinning (thinned and non-thinned) and fertilization (fertilized and non-fertilized) treatments were randomly assigned to the 12 plots in a 2×2 factorial design with three replications. Six plots were thinned in November 1988 by removing every other row of trees and every other tree in the remaining rows leaving 721 trees $ha^{-1}$. The six non-thinned plots had a density of ≈2732 trees $ha^{-1}$. Six plots were broadcast fertilized in April 1989 with diammonium phosphate at 744 kg $ha^{-1}$ (134 kg $ha^{-1}$ N and 150 kg $ha^{-1}$ P), and the remaining six plots were not fertilized. Understory hard-woods, shrubs and vines were removed with a mower. Herbicides were sprayed to control understory vegetation. Steel towers and wooden walkways were constructed in two replications to access the upper and lower portion of live crowns for needle and shoot measurements. In one replication, four light sensors and two solid-state temperature sensors were installed at each of three south-facing locations adjacent to the sample branches selected in the upper and lower canopy (a total of six positions per plot). Multi-directional photosynthetic photon flux density (PPFD) and air temperature ($T_a$) were continuously recorded by a computer-controlled data acquisition system (Gravatt et al., 1997).

### 2.2. Shoot and needle measurements

Fascicle and shoot phenological and morphological data were collected in 1994 (the sixth year after thinning and fertilization treatment). Measurements were conducted in the eight plots (two replications) with six sample trees per plot (a total of 48 trees used). In early March, three south-facing first-order branches in the upper and lower one third of the crown were randomly chosen. Lengths (nearest 0.1 cm) of new flushes on terminal or adjacent lateral shoots were in situ recorded weekly with a meter stick from March through November. Three fascicles on each growing flush shoot were marked and fascicle needle lengths (nearest 0.1 cm, from the tip of the longest needle to the edge of the fascicle sheath) were in situ measured weekly from April through November.

In each month, five fascicles per flush were randomly selected from new flush shoots on the branches near the sample branches used for flush and needle length measurements. These fascicles were removed from the flush shoots, sealed in plastic bags, and morphologically evaluated. Green needles of each fascicle were excised from needle sheaths and measured for total needle volume (nearest 0.01 $cm^3$) with a water displacement approach (Johnson, 1984). The needle samples were oven-dried at 65°C to a constant mass and weighed (nearest 0.01 g). Leaf surface area (NLA) per fascicle was calculated by Eq. (1) (Johnson, 1984):

$$\mathrm{NLA} = 2L(1 + \pi/N)(VN/\pi L)^{1/2} \qquad (1)$$

where $L$ is the cumulative length of the needles per fascicle, $N$ the number of the needles per fascicle, and $V$ the total needle displaced volume per fascicle.

In November, length (nearest 0.1 cm) of the foliated portion of flush shoots was measured in each plot, and the number of fascicles on each foliated flush shoot was counted with a mechanical counter. Fascicle density (number of fascicles per cm of a foliated flush shoot) was calculated by the total number of fascicles per flush divided by the foliated flush length. We observed that the difference between the foliated flush length and total flush length was rather small, because loblolly pine trees retain their needles for about two years (Dougherty et al., 1995) and current-year foliage did not start senescing until the following year. Therefore, leaf area per flush shoot was estimated by the total flush length multiplied by both fascicle density and leaf area per fascicle. Total shoot length (TSL) was the cumulative length of all new flushes on a given shoot and total leaf area per shoot (TSA) was the addition of leaf areas from all these flushes.

### 2.3. Statistical analyses

Means of morphological parameters were computed from the measurements taken in the last week of each month. Monthly means of canopy PPFD and $T_a$ (between 1000 and 1400 h) were calculated from the daily records. Shoot and foliage morphological data were analyzed for each month by the analysis of variance (ANOVA) using a 2×2 factorial split-plot design with two replications (SAS Institute Inc., 1985). Thinning and fertilization were whole-plot factors, whereas crown position was a sub-plot factor. Main and interaction effects of thinning, fertilization and crown position were tested at $p \leq 0.10$ (Steel and Torrie, 1980), because great variability was expected in large-tree crowns under field conditions (Cregg et al., 1989). Least-squares means (LSMEANS) were computed to compare differences between treatment and/or crown means.

To evaluate functional relationships between early-season length and leaf area of fascicles and shoots and canopy PPFD and $T_a$, regression equations were developed with the data (combining the upper and lower crown) collected from March through July. These months were the most active portion of the growing season, because new shoots and foliage expanded rapidly during that period. Test of significance ($p \leq 0.10$) were performed to determine the treatment effects on the slopes and intercepts of regression equations for all treatment combinations. General linear models (GLM) procedures in SAS were used for the regression analysis (SAS Institute Inc., 1985).

## 3. Results

Shoot elongation of first flush shoots in the upper and lower crown began in March and continued through May (Fig. 1(A) and (B)). As second flush shoots initiated in mid-May and third flush shoots elongated later in the year, cumulative shoot length continued to increase through September. Fascicle

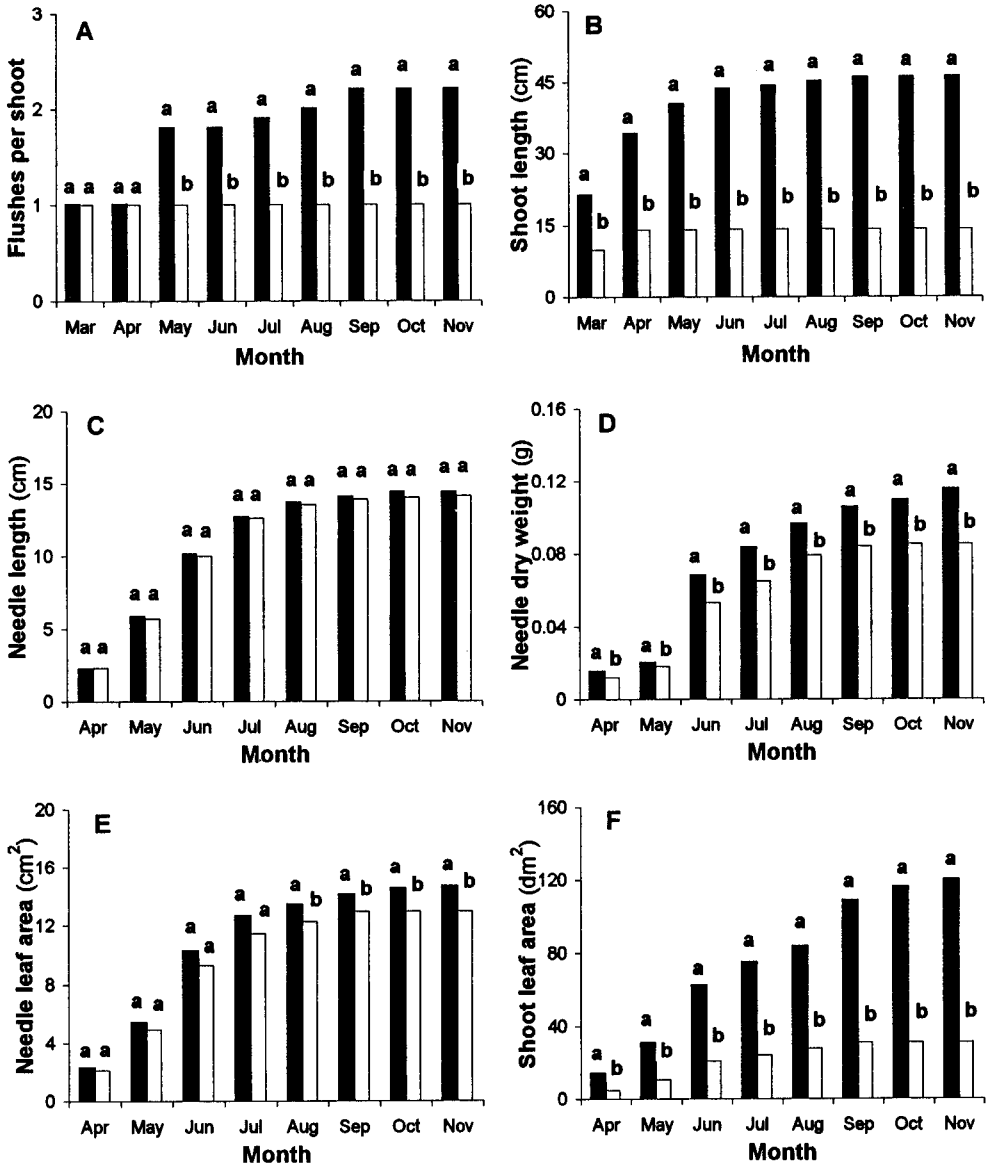


Fig. 1. Crown position effects (■ = upper crown, □ = lower crown) on seasonal changes in (A) number of flushes per shoot, (B) cumulative shoot length, (C) needle length on first flush shoots, (D) dry weight per fascicle, (E) leaf area per fascicle, and (F) leaf area per shoot of loblolly pine trees. Bars not followed by the same letters in a given month differ at $p \leq 0.10$. Each bar is a mean of 24 measurements for a given variable in each month.

needles on first flush shoots started expanding in mid-April, reached 70% of their final length by the end of June, and completed growth in early October (Fig. 1(C)–(E)). Significant differences in shoot and needle measurements were found for crown position (Table 1). Shoots in the upper crown commonly had two or three flushes, whereas only 4% of the lower-crown shoots produced more than one flush (Fig. 1(A)). Upper-crown shoots were significantly longer than lower-crown shoots (Fig. 1(B)). Fascicle needle length of first flush foliage was not statistically different between the two crown levels, but needle dry

Table 1
Probability of $F$-tests for the effects of thinning, fertilization, and crown position on the current-year shoot and needle variables measured in November 1994 [a]

| Source | df | FLG | FLA | NLG | NLA | NWT | NFS | TSL | TSA |
|---|---|---|---|---|---|---|---|---|---|
| Crown (C) | 1 | 0.0087[b] | 0.0026[b] | 0.5596 | 0.0080[b] | 0.0012[b] | 0.0065[b] | 0.0084[b] | 0.0044[b] |
| Thinning (T) | 1 | 0.0086[b] | 0.0772[b] | 0.0199[b] | 0.5714 | 0.4711 | 0.8298 | 0.1200 | 0.0754[b] |
| Fertilization (F) | 1 | 0.5095 | 0.0455[b] | 0.0078[b] | 0.0120[b] | 0.0627[b] | 0.1836 | 0.3733 | 0.0537[b] |
| T×F | 1 | 0.1000[b] | 0.0405[b] | 0.0059[b] | 0.0171[b] | 0.0340[b] | 0.8298 | 0.1680 | 0.0846[b] |
| T×C | 1 | 0.6363 | 0.6582 | 0.3147 | 0.6440 | 0.9859 | 0.5946 | 0.5229 | 0.4679 |
| F×C | 1 | 0.2371 | 0.0546[b] | 0.0140[b] | 0.0387[b] | 0.0080[b] | 0.3904 | 0.2945 | 0.0925[b] |
| T×F×C | 1 | 0.7929 | 0.9359 | 0.1156 | 0.7901 | 0.4604 | 0.8568 | 0.9660 | 0.8931 |

[a] FLG = length of first flushes, FLA = leaf area per first flush, NLG = needle length of first-flush fascicles, NLA = leaf area per first-flush fascicle, NWT = dry weight per first-flush fascicle, NFS = number of flushes per shoot, TSL = total length per shoot, and TSA = total leaf area per shoot.
[b] Significant at $p \leq 0.10$.

weight varied significantly (Fig. 1(C) and (D)). Significant differences in fascicle and shoot leaf area were also observed for crown position, with the upper crown having greater mean values than the lower crown (Fig. 1(E) and (F)).

First flush shoots in the thinned plots elongated an average of 21 cm in the upper and lower crown between March and April, whereas shoots of the non-thinned trees grew 26 cm in flush shoot length (Fig. 2(A)). Monthly needle expansion of first flush fascicles in both treatments averaged 3.3 cm for the period between April and June (Fig. 2(B)). Leaf area of first flush shoots expanded rapidly during this three-month period (Fig. 2(C)). Thinning significantly increased needle expansion of first flush fascicles, but decreased the growth of first flush shoots (Table 1). Thinned trees produced longer fascicle needles and shorter first-flush shoots in the crown than non-thinned trees (Fig. 2(A) and (B)). Second flush shoots in the thinned plots were also significantly shorter than those in the non-thinned plots ($p = 0.0983$). Total leaf area per first flush and per shoot was constantly decreased throughout the crown in response to reduced stand density (Fig. 2(C) and (D)). However, number of flushes per shoot and total shoot length were unaffected by thinning during the sixth growing season following treatment (Table 1).

Fertilization and its interaction with crown position exhibited significant impacts on shoot and fascicle morphological properties in 1994 (Table 1). Upper-crown, first-flush fascicles of the fertilized trees grew 12 cm in needle length, 12.4 $cm^2$ in leaf area, and 0.09 g in oven-dry weight from April through June (Fig. 3(A)–(C)). In contrast, first-flush foliage in the non-fertilized plots expanded 8.4 cm in needle length, 8.2 $cm^2$ in leaf area, and 0.05 g in dry weight during that period. Fertilization also significantly increased needle elongation and leaf area of second flush foliage in the upper crown ($p = 0.0665$ and 0.0074, respectively). Fertilized plots consistently had larger upper-crown leaf area per flush and per shoot than the non-fertilized trees (Fig. 3(D) and (E)). In November, upper-crown leaf area per shoot was 149 $dm^2$ in the fertilized plots, whereas trees in the non-fertilized plots had 91 $dm^2$ of shoot leaf area. However, number of new flushes per shoot and cumulative shoot length of the flush shoots in the upper crown were not statistically different between the two fertilization treatments (Fig. 3(F)).

There was a significant interaction between fertilization and thinning on first flush shoots and their needle morphology within the crown (Table 1). The interaction impact started to be reflected by the growth of first flush shoots in May and their foliage in June. Thinned-fertilized plots had longer first-flush fascicles, and greater needle dry weight and leaf area in the upper and lower crown than the other three treatment combinations by November (Fig. 4(A)–(C)). In contrast, mean length and leaf area on first flush shoots, and total leaf area per shoot in the thinned-nonfertilized plots were substantially smaller throughout the crown than those of the other treatment combinations (Fig. 4(D)–(F)). Subsequent second-flush shoots were

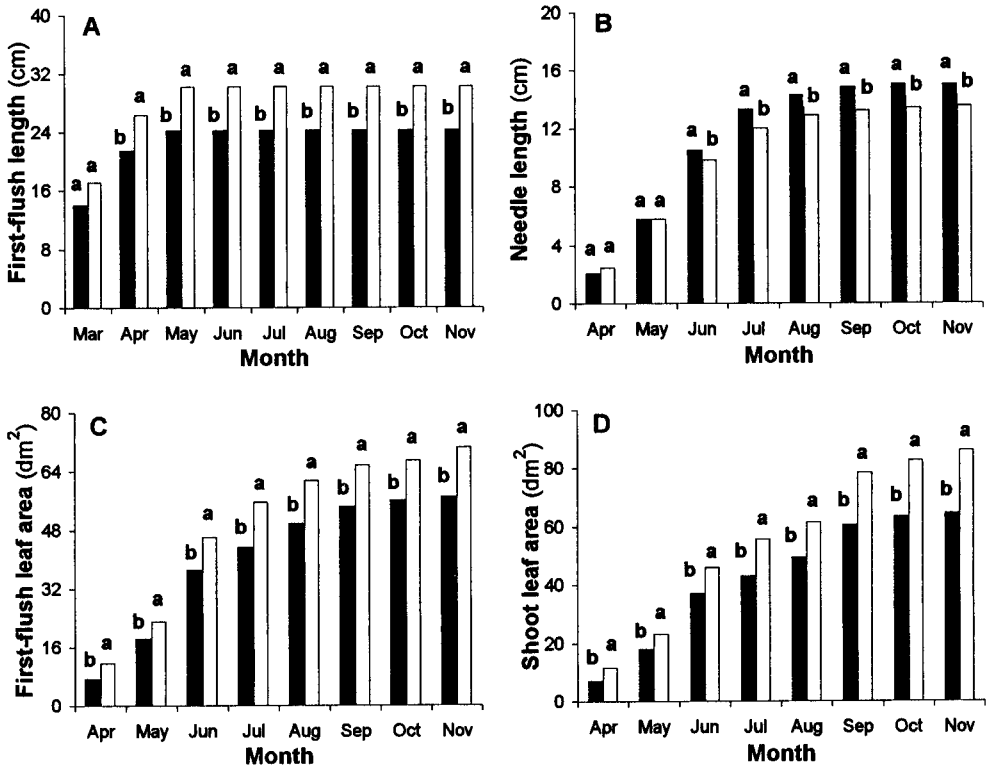


Fig. 2. Thinning effects (■ = thinned plot, □ = non-thinned plot) on seasonal changes in (A) length of first-flush shoots, (B) needle length of first-flush fascicles, (C) leaf area per first-flush shoot, and (D) total leaf area per shoot of loblolly pine trees. Bars not followed by the same letters in a given month differ at $p \leq 0.10$. Each bar represents a mean of 24 measurements for a given variable in each month.

also significantly shorter in the thinned-nonfertilized plots than the other plots ($p = 0.0581$).

Mean multi-directional PPFD (between 1000 and 1400 h) within the canopy ranged from 146 to 1053 μmol $m^{-2}$ $s^{-1}$ between March and June, while mean $T_a$ was 25.4–27.3°C and varied from 16.8° to 33.6°C (Table 2). A strong, linear relationship was found between needle length and leaf area of first flush foliage from April through July and canopy $T_a$ of the previous month in all treatment combinations (Fig. 5(A)–(D), Table 3). Cumulative shoot length was closely correlated with previous-month canopy PPFD (Fig. 6(A)–(D)), whereas total leaf area per shoot largely relied on both PPFD and $T_a$ (Table 3). The slopes and intercepts of all prediction equations were significantly different among the four treatment combinations ($p = 0.0001$). Canopy PPFD and $T_a$ predicted greater length and leaf area for the fascicles and shoots in the fertilized plots than those in the non-fertilized plots as a result of greater slopes in the equations.

## 4. Discussion

Light interception efficiency of an intact shoot is related to the ratio of shoot silhouette area to its total leaf area (Sprugel et al., 1996). When resources (irradiance, temperature, rainfall, and soil moisture and nutrients) are sufficient, forest trees increase leaf area of individual shoots in the crown to achieve the maximum interception of incoming solar radiation and photosynthetic efficiency (Brix, 1982; Sheriff, 1996; Stenberg, 1996). However, foliage production, crown development, and tree growth are often limited by low light availability and nutrient deficiency (Waring et al., 1978; Brix, 1982; Vose and Allen, 1988; Haywood, 1994; Sheriff, 1996).

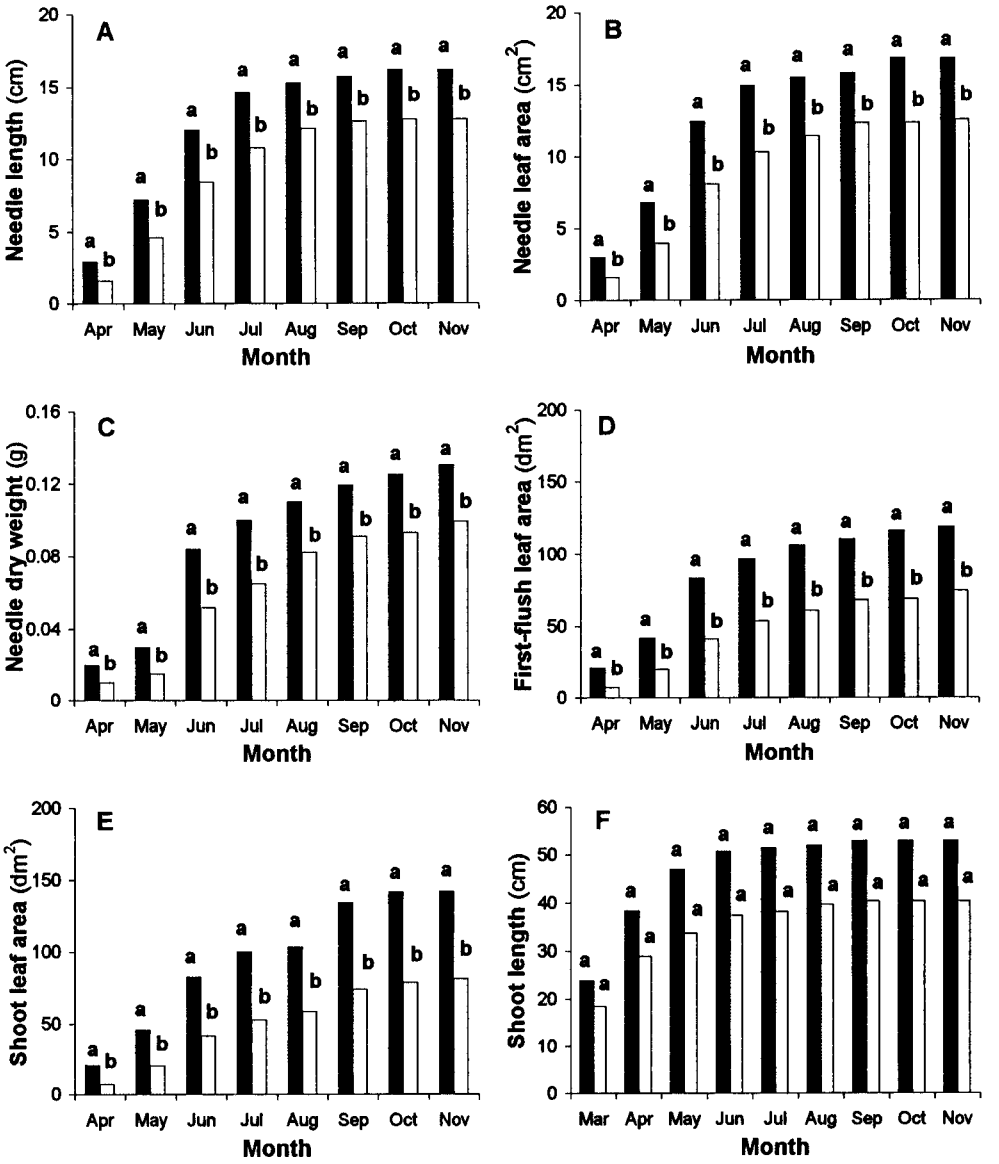


Fig. 3. Fertilization effects (■ = fertilized plot, □ = non-fertilized plot) on monthly changes in (A) needle length of first-flush shoots, (B) leaf area per fascicle, (C) dry weight per fascicle, (D) leaf area per first-flush shoot, (E) leaf area per shoot, and (F) cumulative shoot length in the upper crown of loblolly pine trees. Bars not followed by the same letters in a given month differ at $p \leq 0.10$. Each bar is a mean of 24 measurements for a given variable in each month.

Predicted global climate changes may decrease resource availability within a forest stand (Hansen et al., 1988; Peters, 1990), which will likely cause large reduction in growth and productivity of southern pine forests. Therefore, thinning and fertilization are often used to improve canopy light and soil nutrient conditions for increasing growth and yield (Brix, 1982; Gillespie et al., 1994; Haywood, 1994; Sword et al., 1998).

The soil of our study site is low in available nitrogen and phosphorous (Shoulders and Tiarks, 1983; Allen, 1988). Early field trials showed that tree height and

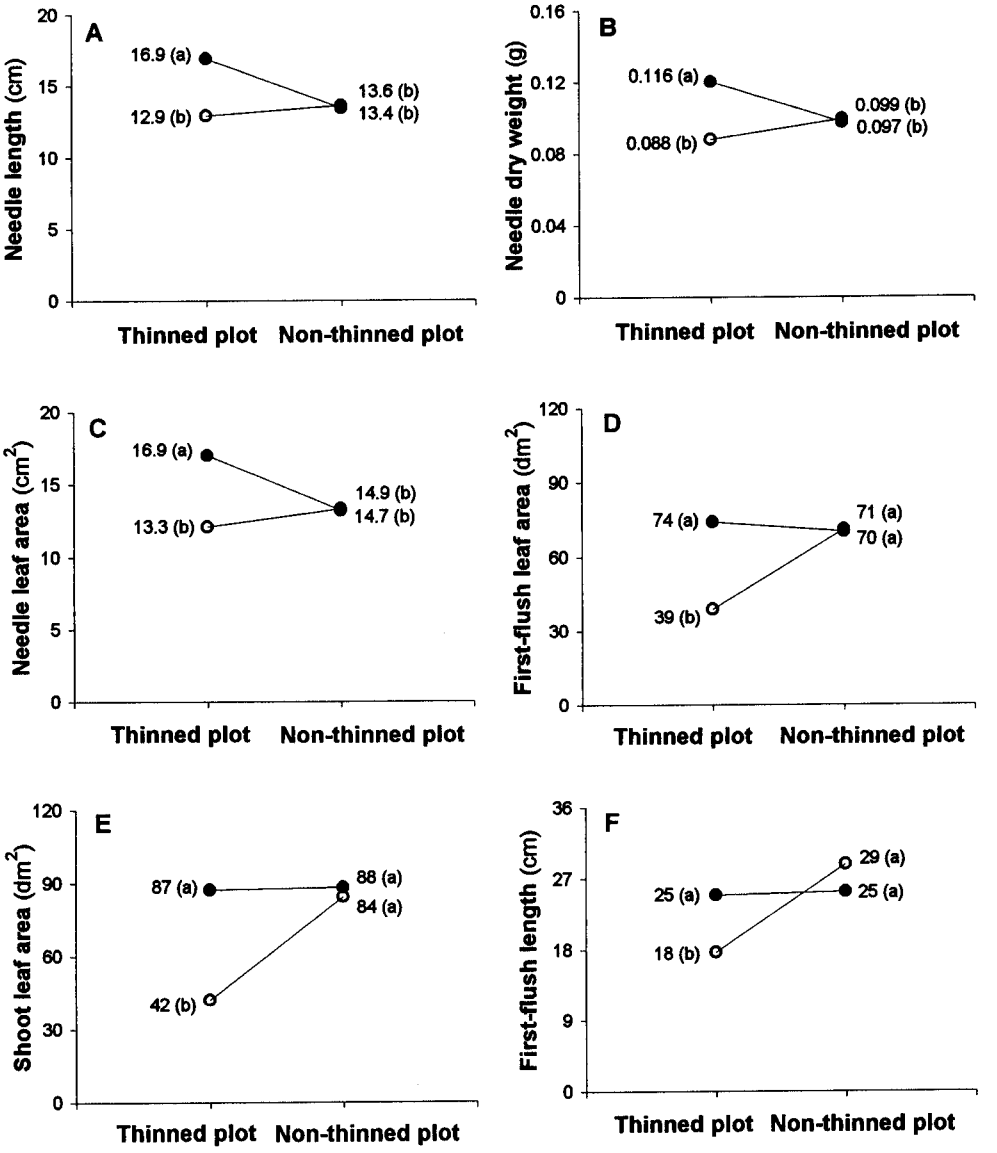


Fig. 4. Interaction effects of thinning and fertilization (● = fertilized, ○ = non-fertilized) on (A) needle length of first-flush shoots, (B) dry weight per fascicle, (C) leaf area per fascicle, (D) leaf area per first-flush shoot, (E) leaf area per shoot, and (F) length of first flushes of loblolly pine trees in November. Means not followed by the same letters in the parentheses differ at $p \leq 0.10$. Each mean represents 12 measurements for a given variable.

diameter increment in the non-fertilized stands responded positively to nitrogen and phosphorous fertilization (Tiarks and Haywood, 1986; Haywood and Tiarks, 1990). In the present study, we observed that seasonal shoot and foliage growth of the non-fertilized trees were limited by low soil fertility. Rainfall and soil moisture supply on the study site were sufficient and needle predawn water potentials remained above −0.70 MPa throughout the year (Tang et al., 1998). Because nutrient supply was insufficient, the expansion of first flush shoots and their foliage in the non-fertilized plots was slow during the early growing season (March–June). Fertilization significantly ameliorated the nutrient-deficient status and

Table 2
Summary of mean canopy light availability and air temperature within the canopy of a loblolly pine plantation between March and June of 1994

| Treatment/Variable [a] | Mean | Minimum | Maximum | Standard deviation | Coefficient of variation (%) |
|---|---|---|---|---|---|
| *Thinned-fertilized plot* | | | | | |
| PPFD | 578.0 | 232.0 | 949.0 | 281.0 | 48.6 |
| $T_a$ | 25.4 | 17.9 | 32.4 | 5.0 | 19.8 |
| *Thinned-nonfertilized plot* | | | | | |
| PPFD | 709.0 | 349.0 | 1053.0 | 232.0 | 32.7 |
| $T_a$ | 27.3 | 19.6 | 33.6 | 4.5 | 16.6 |
| *Nonthinned-fertilized plot* | | | | | |
| PPFD | 527.0 | 146.0 | 942.0 | 306.0 | 58.1 |
| $T_a$ | 26.0 | 17.4 | 33.5 | 5.3 | 20.4 |
| *Nonthinned-nonfertilized plot* | | | | | |
| PPFD | 608.0 | 181.0 | 932.0 | 268.0 | 44.2 |
| $T_a$ | 25.8 | 16.8 | 33.1 | 5.6 | 21.7 |

[a] PPFD = photosynthetic photon flux density ($\mu$mol $m^{-2}$ $s^{-1}$) between 1000 and 1400 h, and $T_a$ = air temperature (°C) between 1000 and 1400 h.

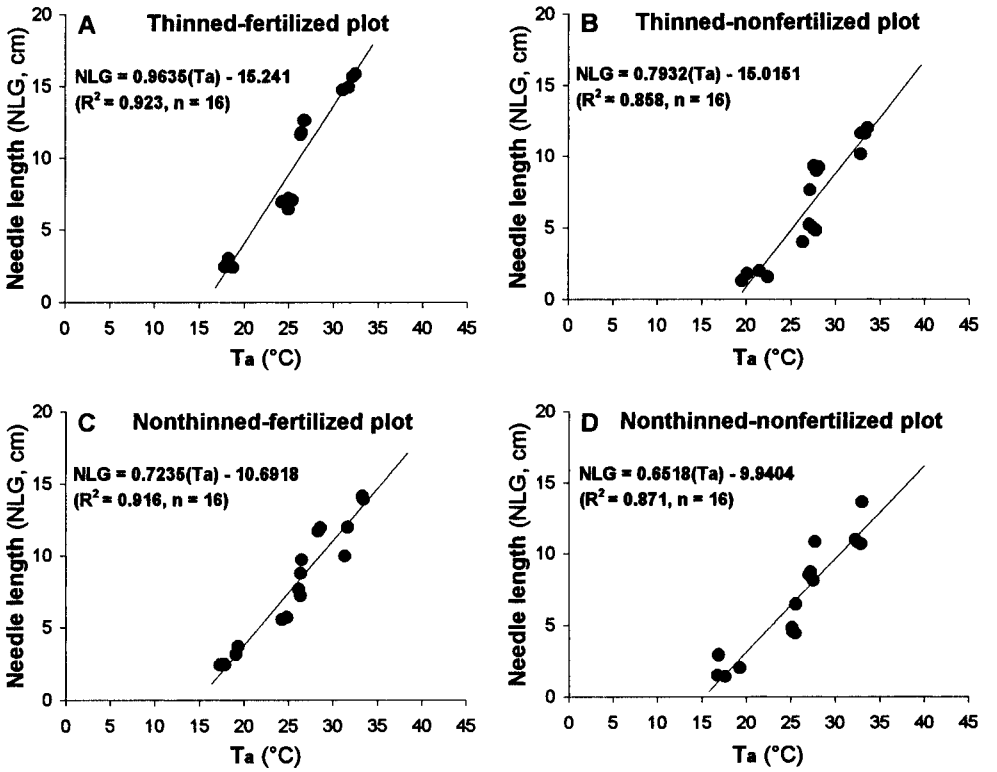


Fig. 5. Relationship between needle length (NLG) of loblolly pine first-flush foliage from April through July and previous-month air temperature ($T_a$) within the canopy of the four treatment combinations.

Table 3
Relationships between fascicle and shoot leaf area from April through July and previous-month light availability and air temperature within the canopy of a loblolly pine plantation ($n = 16$)

| Variable/Treatment | Equation [a] | $R^2$ |
|---|---|---|
| *Needle leaf area (NLA)* | | |
| Thinned-fertilized plot | NLA = 0.8232($T_a$) − 12.4504 | 0.778 |
| Thinned-nonfertilized plot | NLA = 0.6819($T_a$) − 12.7914 | 0.779 |
| Nonthinned-fertilized plot | NLA = 0.7303($T_a$) − 11.2016 | 0.874 |
| Nonthinned-nonfertilized plot | NLA = 0.6118($T_a$) − 9.4146 | 0.875 |
| *Shoot leaf area (TSA)* | | |
| Thinned-fertilized plot | TSA = 0.0785(PPFD) + 2.7816($T_a$) − 79.7610 | 0.776 |
| Thinned-nonfertilized plot | TSA = 0.0266(PPFD) + 2.1058($T_a$) − 59.7617 | 0.584 |
| Nonthinned-fertilized plot | TSA = 0.0815(PPFD) + 2.5078($T_a$) − 70.6489 | 0.806 |
| Nonthinned-nonfertilized plot | TSA = 0.0293(PPFD) + 2.5068($T_a$) − 51.7418 | 0.657 |

[a] NLA = needle leaf area per first-flush fascicle ($cm^2$), TSA = total leaf area per shoot ($dm^2$), PPFD = photosynthetic photon flux density ($\mu mol\ m^{-2}\ s^{-1}$) between 1000 and 1400 h, and $T_a$ = air temperature (°C) between 1000 and 1400 h.

stimulated flush shoot growth and leaf development in the upper crown between March and June. At the end of the growing season, upper-crown shoot length was increased by 30% and shoot leaf area was increased by 64% in the fertilized plots. These findings indicate that fertilization continued to enhance early-season shoot and needle expansion, and annual leaf area production six years after treatment.

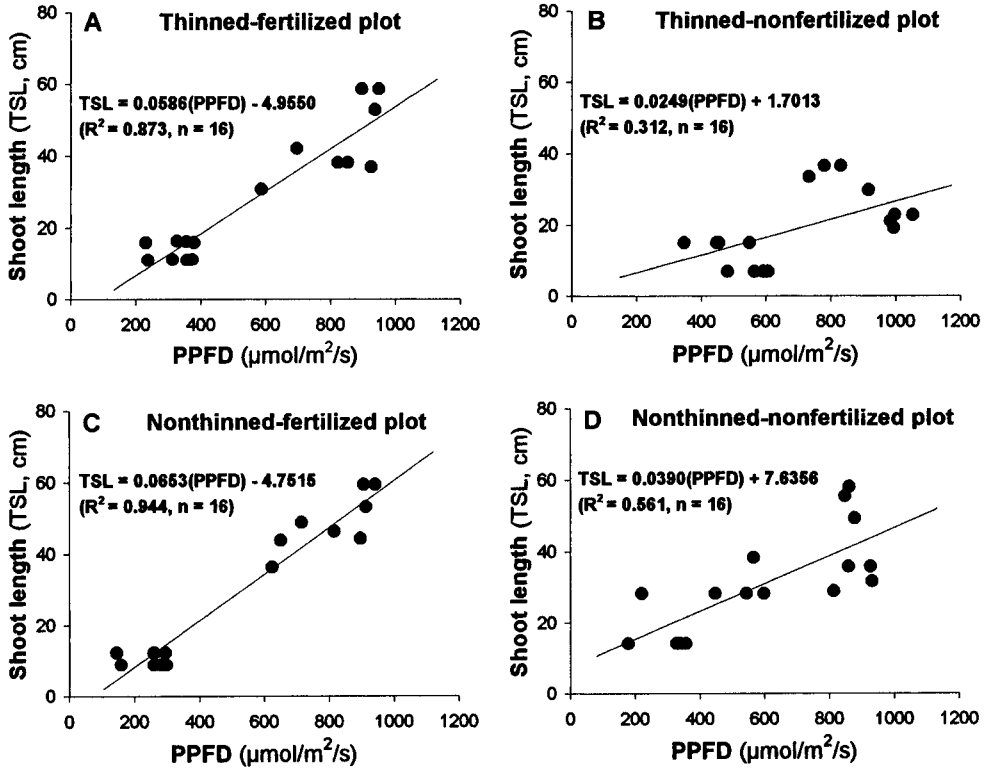


Fig. 6. Relationship between cumulative shoot length (TSL) of loblolly pine from April through July and previous-month light availability (PPFD) within the canopy of the four treatment combinations.

Photosynthetic production primarily depends on the amount of foliage and the rate of net photosynthesis per unit of leaf surface area (Teskey et al., 1987). Forest growth and productivity are closely associated with seasonal leaf area production and photosynthate distribution (Dickmann, 1971; Larson, 1980; Isebrands, 1982; Michael et al., 1988). When current-year expanding needles of loblolly pine reach 55% of the final length, their photosynthetic capacity exceeds that of one-year-old foliage (Radoglou and Teskey, 1997). Photosynthate produced by early-season foliage is allocated acropetally for the development of subsequent flush shoots in the same year (Dickson, 1987; Tschaplinski and Blake, 1989). Thus, rapid leaf area expansion of new foliage early in the growing season is very important for photosynthate production and late-season shoot and needle growth. Data of this study show that fascicle needles on first flush shoots already achieved 70% of their final length and 65% of their final leaf area by the end of June. The fertilized trees produced 83 $dm^2$ of total leaf area per shoot in the upper crown at that time, whereas the non-fertilized trees maintained only 41 $dm^2$ of shoot leaf area. By November, upper-crown needle size and leaf area on second flush shoots were significantly increased by fertilization. Total leaf area of the upper-crown shoots was also substantially increased in the fertilized plots. Earlier in a related study, Haywood (1994) reported positive responses of tree height, diameter and stand basal area four years after fertilization, and Sword et al. (1996) reported increased fine root growth five years after treatment. Increased leaf area by fertilization found in this study provides an explanation for the observed responses in tree size, stand production, and root growth. Such relationships between fertilization, shoot development, foliage biomass, and aboveground yield have also been found by other investigators (Brix, 1981, 1982; Vose and Allen, 1988; Gillespie et al., 1994; Teskey et al., 1994; Sheriff, 1996).

New flush shoots in both thinned and non-thinned plots elongated rapidly early in the 1994 growing season. By the end of June, cumulative shoot length of first- and second-flush shoots reached 98% of the annual length in the thinned plots and 94% in the non-thinned plots, whereas total leaf area per shoot was only 57% and 53% of the final value, respectively. The residual thinning effect was found to influence foliage expansion in the upper and lower crown during the sixth post-treatment year. When compared to the non-thinned plots, first flush needles of the trees in the thinned plots were longer. However, thinning appeared to constantly reduce shoot elongation and leaf area of first flush shoots in the crown throughout the year. Results from this study are consistent with the findings by Brix (1981) who investigated branch development and foliage production of 24-year-old Douglas-fir trees five years after thinning. He also found a substantial increase in number of shoots in response to reduced stand density. However, contrary to his results, we found that number of flushes per shoot did not vary significantly between the two thinning treatments six years after treatment, because crown closure had started to occur in the thinned plots. In addition, the thinned trees were beginning to show large crown-level differences in light availability and needle net photosynthesis (Gravatt et al., 1997; Tang et al., 1998). Therefore, re-thinning is needed to stimulate shoot development and foliage physiological activity within the crown.

Fertilization and thinning together substantially increased leaf area production of individual shoots throughout the crown. This was because the thinned-fertilized treatment significantly increased (1) irradiance and growing space within the canopy, (2) first-flush shoot length by 39% and leaf area by 127% during the first half of the year (March–June), and (3) needle size and leaf area of first flush foliage from July through November. At the end of the growing season, trees in the thinned-fertilized plots had 54% greater shoot length and 107% more shoot leaf area than those in the thinned-nonfertilized plots. These observations strongly suggest that as canopy environmental conditions are improved in the thinned stands growing on the poor sites, nutrient deficiency becomes a major factor limiting shoot expansion and leaf area development. Thus, fertilizers need to be applied soon after thinning. The relationship between shoot development, tree growth and resource availability within a forest stand also implies that silvicultural manipulation may provide an useful means to improve potentially detrimental effects of global climate changes on southern pine forests.

Recent studies suggest that there is great variability in micro-environmental conditions within the canopy of coniferous stands (Jordan and Smith, 1993; Stenberg, 1996). Large variation in needle physiology and

morphology, shoot geometry and branch structure is observed vertically in the canopy, primarily due to canopy light availability (Niinemets and Kull, 1995; Sprugel et al., 1996; Brooks et al., 1994; Gravatt et al., 1997; Tang et al., 1998). Differences in shoot structure and needle geometry within the crown are closely associated with variation in the utilization of intercepted light for photosynthetic production and tree growth (Leverenz and Hinckley, 1990; Jordan and Smith, 1993; Niinemets and Kull, 1995; Sprugel et al., 1996). Similar to these findings, data from the current study illustrate a close relationship between early-season shoot and needle expansion and canopy light gradient. For example, for an irradiance increase of 100 $\mu$mol $m^{-2}$ $s^{-1}$ vertically within the crown, total shoot length tended to be increased by 13–22% (2.4–6.5 cm) in all treatment combinations. Total leaf area per shoot was also increased, which may increase the utilization efficiency of intercepted solar radiation and ultimately tree growth and stand productivity (Leverenz and Hinckley, 1990; Brooks et al., 1994; Sprugel et al., 1996).

Annual air temperature is predicted to increase 2–3°C for the southern states (Cooter et al., 1993), which may influence resource availability, shoot phenology, foliage physiology, root development and tree growth within a forest stand (Sword et al., 1998). Results from this study suggest that during the Spring and early Summer a small temperature elevation may favor foliage growth and development. Given that annual $T_a$ rises by 2°C with unchanged canopy PPFD and adequate rainfall, our equations predict that fascicle needle size and leaf area tend to be increased appreciably. Total leaf area per shoot will be increased by 15–23%. In another study of the same species, Teskey (1997) concluded that a 2°C increase in $T_a$ had little effect on foliage expansion, branch growth, and needle net photosynthesis. It is, therefore, likely that a 2–3°C increase in seasonal temperature will not limit shoot development and foliage growth of forest trees during the Spring and early Summer. The range of temperature fluctuation may become a more important factor than temperature rise, at least for early-season growth. During the Summer, extremely high temperature can limit realized growth by reducing photosynthetic production of already existing foliage. Long-term field studies are needed to investigate phenological, morphological, and physiological responses of southern pine forests to extreme high temperatures and severe drought under silvicultural treatment conditions.

## 5. Conclusions

Under field conditions, rapid growth of new flush shoots and foliage occurred during the early part of the growing season. Cumulative shoot length between April and July was closely correlated with previous-month light availability within the canopy, whereas needle length was linearly related to air temperature. Total leaf area of individual shoots was a function of both previous-month irradiance and temperature. Fertilization continued to produce a positive effect on early-season shoot and fascicle expansion in the upper crown six years after treatment. Mean length and leaf area of upper-crown first flush shoots were consistently increased by fertilization. Although the residual thinning effect stimulated needle elongation, it caused a significant reduction in first-flush shoot length and leaf area throughout the crown. Moreover, fertilization combined with thinning favored seasonal growth of new flush shoots and foliage in the upper and lower crown. Fascicle needle size, dry mass, and leaf area on first flush shoots were all enhanced by the thinned-fertilized treatment in the early growing season. As a result, total leaf area of shoots was substantially increased by the end of the growing season. Our data suggest that early-season shoot expansion, crown development, and foliage production of large pine trees are closely associated with canopy and soil environmental factors within a forest stand. Lengthy droughts or unusual weather conditions in the early growing season may impact this relationship. Global climate change may also influence these factors and cause potential stresses on growth and productivity of southern pine forests. However, stand environmental and growth conditions may be significantly improved by silvicultural manipulations such as thinning and fertilization.

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